MORPHOLOGY OF THE FORELIMB OF THE MOLE (SCALOPS AQUATICUS, L.) IN RELATION TO ITS FOSSORIAL HABITS

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INTRODUCTION

The common American mole (*Scalops aquaticus*, Linnaeus) is a completely fossorial animal which spends its entire existence in underground tunnels of its own construction. The fossorial adaptations which enable the mole to lead its subterranean mode of existence have been described, at least in a general way, by numerous authors. The most comprehensive description of the morphology of the mole is the work of Dobson ('82), whose description, however, concerns primarily the European mole (*Talpa europea*) and the star-nosed mole (*Condylura cristata*), although frequent references are made to other species including *Scalops aquaticus*. Slonaker ('20), in addition to summarizing the results of former investigators which, as he pointed out, are more or less fragmentary and scattered promiscuously throughout the literature, also described certain adaptive modifications in the American mole, particularly the osteology of the forelimb and pelvis and correlated these with the animal's habits and environment.

The objectives aimed at in the present paper are threefold, namely: (1) a more detailed description of the osteology of the forelimb of the mole than has heretofore been given; (2) a description of the articulations of the forelimb, including articular surfaces involved, ligaments with their attachments and adaptive modifications, the normal position assumed by each segment of the forelimb and the kinds of movements permitted at the various joints; and (3) a description of the musculature including the arrangement, attachments (origins and insertions), actions and nerve supply of the muscles, with the view to correlating these features with the peculiar functions which the forelimb performs in the process of constructing the underground tunnels.

The mole is especially adapted to a life spent entirely beneath the surface of the ground in burrows where it secures not only shelter but also its food. Its neck appears to be so short that it is almost imperceptible. However, the shortness of the neck is more apparent than real and is due to the fact that the forelimb has shifted forward rather than to an actual shortening of the cervical region of the vertebral column, since this region contains the characteristic number of vertebrae typical of the mammals, namely, seven. The forward shift of the forelimb is the result of the pre-sternum or manubrium having elongated into a keel-shaped bone, to the anterior extremity of which the short clavicles articulate (fig. 1C). As a consequence, therefore, of the forelimbs having shifted forward upon the neck,

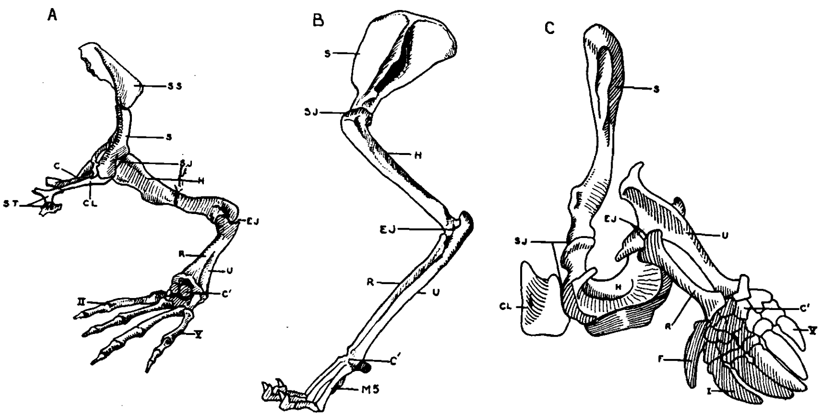

FIG. 1. A—Anterior (cranial) view of articulated forelimb of frog; B—lateral view of articulated forelimb of cat; C—anterior view of articulated forelimb of mole. These illustrations were made with disregard of relative size. (Interpretation of legends is given in list of abbreviations, page 41.)

not only is the latter apparently shortened but the shoulder-joints are brought nearer each other thus causing an apparent shortening of the forelimbs, while preserving at the same time their normal leverage. These are important fossorial adaptations which enable the mole to economize in working room, since a long neck and long, projecting forelimbs would be mechanical disadvantages to a burrowing animal working in close quarters.

The bones of the forelimb, especially the clavicle, scapula and humerus, are singularly developed and modified rendering it difficult to homologize certain of their configurations with those of other mammals. They are for the most part quite strong and exhibit prominent processes for the attachment of the powerful muscles which serve to put the forelimbs into action.

The manus is especially modified to form an effective digging mechanism. It is not only strong and broad, but the digits are provided with strongly developed nails sharpened at their tips. Broadening of the manus has been accomplished (1) by a relative increase in the width of the bones of the manus, (2) by the development of an accessory bone, the so-called falciform bone, situated external to the pollex and (3) by the abduction (spreading apart) of the digits which are webbed throughout the greater part of their length. The position of the manus is such as to render it favorable for digging and makes it poorly adapted for progression on a hard supporting surface, as is evidenced by its awkward scraping movements when the animal attempts to scurry to safety when placed on such a surface.

Comparison of the articulated forelimb of the mole when at rest with that of typical tetrapod mammals reveals that the position of its segments has been greatly altered to meet the demands placed upon it. In the more primitive tetrapods, as for example, the amphibians (fig. 1A), the brachium is abducted, that is directed almost horizontally outward at right angles to the longitudinal axis of the body such that the elbow-joint projects laterad; the antibrachium is semi-flexed and semi-pronated and the manus is slightly extended at the wrist-joint so that the palm rests upon the ground. In the typical forelimb of mammals as in the cat for example (fig. 2B), the brachium is swung backward (flexed) and adducted so that the elbow-joint lies close to the side of the body and is directed caudad; the antibrachium is semi-flexed and semi-pronated and the manus is extended at the wrist-joint. As regard the normal position of the tetrapod shoulder-girdle the scapula which, unlike the clavicle, is constant in occurrence, is a flat, triangular bone applied against the lateral aspect of the thorax in an oblique direction, such that its glenoid cavity is directed ventrad and more or less craniad, its superior or vertebral border dorsad and somewhat caudad.

In the forelimb of the mole (fig. 3C) the brachium has assumed a more abducted position than that of the amphibians and in addition has swung forward (extended) in such a manner that the elbow-joint is directed antero-laterad. Moreover the antibrachium is apparently so greatly pronated that the palm of the manus faces postero-laterad. The apparent extreme pronation of the antibrachium is the result of the humerus having undergone considerable medial rotation, as is evident by the spiral course of the nerves to the forelimb (figs. 14, 15), and of the head of the humerus having shifted to its dorsal surface so that its neck and shaft form an angle of about 90°, rather than actual pronation of the antibrachium as is evident from the position of the radius and ulna with respect to each other (fig. 3C).

As a result of the torsion undergone by the humerus its proper lateral border faces antero-mediad and its medial border postero-laterad, while, as a result of extension and abduction, its proximal extremity is directed postero-mediad and its distal extremity antero-laterad. That the radius and ulna have not actually undergone much pronation is evidenced by the fact that they lie parallel with each other and are uncrossed. Moreover, the ulna is situated in a position lateral to that of the radius, a very unusual position due to the torsion of the humerus, while the proper dorsal surface of both radius and ulna faces antero-laterad thus resulting in the radial border of the manus facing postero-laterad and its ulnar border antero-mediad, such that the pollex points ventrad and caudad and the palm faces laterad and caudad. A simulation of the peculiar position assumed by the forelimb of the mole may be gained in the superior extremity of man by performing the following movements: swinging forward and abduction of the brachium at the shoulder-joint to a ninety-degree angle; semiflexion of the antibrachium at the elbow-joint and extreme medial rotation of both the brachium and antibrachium.

Concomitant with the favorable position assumed by the free forelimb of the mole in its burrowing habits are the peculiar morphological modifications and position of the bones of the shoulder-girdle. When the mole is engaged in excavating its burrow considerable lateral pressure is exerted upon the forelimb—hence the importance of a powerful shoulder-girdle to resist the great muscular strain. The clavicle, unlike that of other mammals in which it is present, articulates with the humerus, but not with the scapula. It is so constructed and situated as to resist this lateral pressure and to furnish a strong and stable fulcrum upon which the humeral lever swings.

The scapula exhibits remarkable morphological adaptations in its shape as well as its position. In conformity with the change in position of the humerus as well as its head the shape and position of the scapula have likewise been altered. Thus it has undergone a posterior rotation so that its proper dorsal border is directed caudad, its anterior border dorsad, its posterior border ventrad and the glenoid cavity craniad. Moreover, as a consequence of the humerus having shifted forward due to the forward extension of the manubrium, the scapula has become greatly elongated and has come to lie along the side of the neck and dorsal to the first five or six ribs.

OSTEOLOGY

The **Clavicle** (figs. 1C, 4) is extraordinarily short and somewhat cuboidal in form. Its proximal or medial extremity is marked by an elliptical-shaped concavity which articulates with a reciprocal-shaped convexity on the anterior extremity of the presternum or manubrium. Its distal or lateral extremity presents an oval shaped, concave articular surface for articulation with a similar shaped convex articular surface (clavicular facet) on the greater tuberosity of the humerus (figs. 1C, 5, 6). Its anterior surface is smooth and gives origin to the deltoid muscle (fig. 12). Extending from the anterior to the posterior surface is a foramen which transmits a blood-vessel. On the ventral border is a slight projection, the subclavian tubercle, into which the subclavius muscle (fig. 12) is inserted. Into the posterior aspect of the lateral extremity is inserted the pectoralis minor muscle (fig. 12) and to its superior aspect is attached the acromioclavicular ligament (fig. 15).

The **Scapula** (figs. 1C, 2, 3) is remarkably slender and elongated. Its posterior (original dorsal or vertebral) border is short, rounded and roughened for the attachment of muscles, namely, the trapezius anterior, rhomboids, levator scapulae and serratus (magnus) anterior muscles (fig. 13). Its medial or costal surface presents a slight elongated depression, the subscapular fossa, from which the subscapularis muscle (fig. 15) arises. Its lateral or external surface presents numerous bony configurations; one of these, the spine, into which the trapezius posterior (fig. 13) inserts, is but slightly developed; the supraspinous fossa is narrow, shallow and elongated and furnishes the origin for the supraspinatus muscle (fig. 15); the infraspinous fossa is deeper and marks the point of origin of the infraspinatus muscle (fig. 15). The latter fossa is bounded above and below by ridges, the lower giving rise to the teres minor muscle (fig. 15) and to the long or scapular head of the triceps muscle (figs. 13–15).

A coracoid process is not in evidence. However, the acromion process is well marked and somewhat roughened for the attachment of the acromioclavicular ligament.

The ventral (original posterior) border of the scapula is rounded and gives origin to the teres major muscle (figs. 13–15). The glenoid fossa, which receives the head of the humerus, is shallow and elongated transversely. Near it on the ventral border is a slight projection, the infraglenoid tubercle, from which the biceps brachii muscle (figs. 12, 15) arises.

The **Humerus** (figs. 1C, 5, 6) is most unusual in shape and is characterized by its shortness, the great development of its processes for muscular attachments and by the presence of an articular surface (clavicular facet) for articulation with the clavicle. The head is elongated transversely and projects posteriorly. The neck, into which the supraspinatus muscle inserts, forms an angle with the shaft of about 90°.

The proximal extremity is marked by the peculiarly shaped tuberosities. The greater (external) tuberosity presents a large oval shaped articular facet (clavicular facet) for the lateral extremity of the clavicle and a sharp spinous process which projects distally. From the posterior aspect of the former arises the deep portion of the external head of the triceps (fig. 14) and into it is inserted the infraspinatus muscle. From the spinous process arises the superficial portion of the external head of the triceps and into it inserts the teres minor muscle (fig. 15). The greater tuberosity overhangs a deep fossa which extends upward under the clavicular facet and is continuous on the lateral border with a spiral groove. This fossa and groove, which curves forward to the ventral surface, give origin to the brachialis muscle (figs. 12, 15).

The lesser (internal) tuberosity consists of two laminae of bone which fuse to form the so-called bicipital ridge and the intertubercular (bicipital) groove. Into the ridge are inserted the subscapularis muscle (fig. 15) and the posterior superficial and deep portions of the pectoralis major muscle (figs. 12, 15). The groove is peculiar in that it is transformed into a closed canal for the passage of the long, slender tendon of origin of the biceps muscle (fig. 15). Distal to these laminae is a notch, which separates them from a crest-like process (L3) into which is inserted the conjoined tendon of the latissimus dorsi and teres major muscles (figs. 12, 15). The tendon of origin of the biceps passes through this notch to gain the ventral surface of the humerus.

The ventral surface presents proximally a large, smooth triangular surface bounded externally by the deltoid tuberosity and internally by the pectoral ridge. Into the former inserts the deltoid muscle and into the latter are inserted the anterior superficial and deep portions of the pectoralis major muscle (figs. 12, 15). The dorsal surface is marked by a pronounced, obliquely situated, groove from which the internal head of the triceps muscle (figs. 12, 13, 15) arises.

The distal extremity presents a number of processes, two of which are articular for the bones of the antibrachium, while the others serve for muscular attachments. The lateral epicondyle consists of a sharp spinous process which gives origin to the anconeus externus muscle (fig. 14) and the dorsal or extensor group of muscles of the antibrachium (figs, 13, 15). Just internal to this is the smooth, oval shaped capitulum for articulation with the proximal extremity of the radius and above the capitulum is a slight depression, the radial fossa, for the reception of the margin of the sigmoid cavity on the proximal end of the radius during extreme flexion of the elbow-joint.

The medial epicondyle is marked by a spinous process proximally and a facet-like process distally. From the former arise the anconeus internus, pronator teres and palmaris longus muscles, while to the

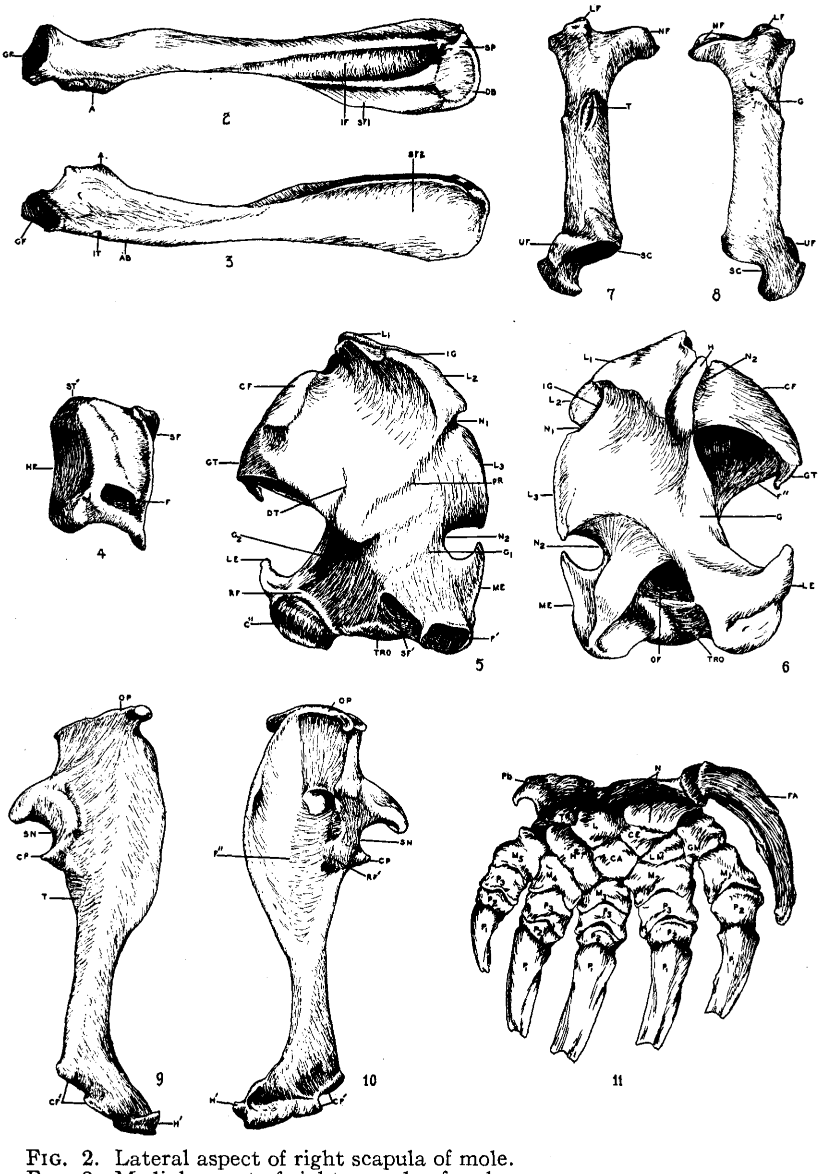

FIG. 2. Lateral aspect of right scapula of mole.
FIG. 3. Medial aspect of right scapula of mole.
FIG. 4. Anterior (cranial) aspect of right clavicle of mole.
FIG. 5. Ventral (original anterior) aspect of right humerus of mole.
FIG. 6. Dorsal (original posterior) aspect of right humerus of mole.
FIG. 7. Ulnar (original medial) aspect of right radius of mole.
FIG. 8. Medial (original lateral) aspect of right radius of mole.
FIG. 9. Lateral (original medial) aspect of right ulna of mole.
FIG. 10. Medial or radial (original lateral) aspect of right ulna of mole.
FIG. 11. Dorsum of right articulated manus of mole.

(Interpretation of legends is given in list of abbreviations, page 41.)

latter is attached the tendinous flexor digitorum profundus (fig. 14). Adjacent to the medial epicondyle on the ventral surface are the supracondylar foramen, which transmits the median nerve, and a slight coronoid fossa for the reception of the coronoid process of the ulna (fig. 10) during extreme flexion of the elbow-joint, while on the dorsal surface is the deep olecranon fossa for the reception of the posterior margin of the semilunar notch of the ulna during extreme extension of the elbow-joint.

The **Radius** (figs. 1C, 7, 8) is also greatly modified. Thus its proximal extremity presents a sigmoid cavity for articulation with the capitulum of the humerus rather than a circular disc or head as in most higher forms. On its medial aspect is a small articular facet for articulation with a corresponding facet on the adjacent margin of the proximal extremity of the ulna. The medial surface of the shaft is roughened, forming what may be termed the bicipital tuberosity for the insertion of the biceps brachii muscle (figs. 12, 15), near which is the point of insertion of the pronator teres muscle (fig. 14). The lateral surface presents an obliquely directed groove through which the tendon of the extensor ossi metacarpi muscle (fig. 15) glides. The distal extremity is greatly expanded from lateral to medial and bears two articular surfaces, a lateral one for articulation with the navicular (scaphoid) bone and a medial one for articulation with the lunate (semilunar) bone. Little or no articulation occurs between this extremity of the radius and that of the ulna.

The **Ulna** (figs. 1C, 9, 10) exhibits still greater fossorial adaptations. Its proximal extremity is marked by a greatly pronounced olecranon process which is expanded at its free end and is keeled throughout its length, as a result of which leverage of the extensor muscles of the elbow-joint is greatly increased. Into this process are inserted the anconeus externus and internus (figs. 14, 15) and the triceps (figs. 14, 15) muscles, while it serves for the point of origin of the flexor (fig. 14) and extensor (fig. 13) carpi ulnares, the flexor digitorum sublimis (fig. 14), the extensor pollicis et indicis (fig. 15) and the extensor ossi metacarpi (fig. 15) muscles. The semilunar notch is so deep and narrow that it almost approximates a hollow cylindrical articular surface which tends to increase the stability of the elbow-joint. It is bounded proximally by a hook-like process of the olecranon and distally by the coronoid process. Just distal to the latter on the volar (anterior) surface is a roughened area, the ulnar tuberosity, into which the brachialis muscle (fig. 15) is inserted. As mentioned above, on the lateral margin of the semilunar notch is a small articular facet for articulation with a corresponding one on the medial margin of the sigmoid cavity of the radius. The distal extremity presents laterally a notched articular surface, which articulates with the triquetral (cuneiform) bone, and medially a hook-like articular surface, which articulates with the pisiform bone.

The **Manus** (figs. 1C, 11) is composed of the typical divisions, namely, the carpus, metacarpus and digits. The carpus consists of two rows of bones, a proximal row containing the navicular (scaphoid), lunate (semilunar), triquetral (cuneiform) and pisiform, and a distal row containing the greater multangular (trapezium), lesser multangular (trapezoid), the central (centrale or intermedium), the capitate (os magnum) and hamate (unciform). The palmar aspect of the carpus is smooth and is bounded laterally by a ridge on the navicular bone and medially by the pisiform bone, thus forming a somewhat shallow groove for the passage of the tendons of the volar or flexor group of antibrachial muscles.

The metacarpal bones are five in number and quite short. They are somewhat wedge-shaped with their palmar surfaces reduced to narrow transverse crests in which are grooves for the tendons of the flexor digitorum profundus muscle. The phalanges are short, broad and flattened, with the typical number present. The distal or terminal phalanges are bifid and provided with long, broad nails sharpened at their tips. The falciform bone lies to the lateral side of the pollex and is attached proximally to the navicular bone while its distal free extremity extends to the base of the proximal phalanx of the pollex.

ARTICULATIONS

The **Sternoclavicular-joint** is surrounded by an articular capsule which is reinforced dorsally and ventrally by accessory ligaments. An articular disc is not present as in man. The movements permitted at this joint are protraction (swinging forward) and retraction (swinging backward) of the clavicle.

The **Shoulder-joint** (fig. 3C) is a double one, being composed of a humero-scapular and a humero-clavicular element. Since the humerus typically articulates only with the scapular element of the shoulder-girdle, it is apparent that the significance of this double articulation in the mole is that it adds stability and serves to produce a firm support for the humerus to swing upon as a lever during the digging movements. The clavicle of the mole therefore does not serve as a prop to support the scapula as in man, but rather as a fulcrum on which the humerus swings.

The ligaments involved in this articulation are two articular capsules, one for each part of the joint. These are reinforced dorsally and ventrally by accessory bands of fibers. In addition the strong acromioclavicular ligament (fig. 15) adds further strength and security. It is attached to the acromion of the scapula and to the dorsal aspect of the lateral end of the clavicle. The attachments and size of this ligament would seem to indicate that it serves to brace the proximal end of the scapula against the lateral end of the clavicle and, therefore, compensates for the lack of an articulation between these bones.

Due to the nature of the articular surfaces composing the shoulder-joint it is probable that the movements permitted at the humero-clavicular portion are swinging forward (extension) swinging backward (flexion), elevation sideward (abduction) and depression to the side (adduction), whereas it is possible that only abduction and adduction occur at the humero-scapular portion. It is doubtful whether rotation of the humerus takes place at either of these points, since the nature of the articular surfaces and arrangement of the ligaments, especially the acromioclavicular, would seem to render this movement impossible.

The **Elbow-joint** (fig. 3C) is likewise a double articulation, consisting of humero-ulnar and humero-radial elements. As a result of the nature of the articular surfaces involved great strength and security are obtained here. In addition to the articular capsule, with which each

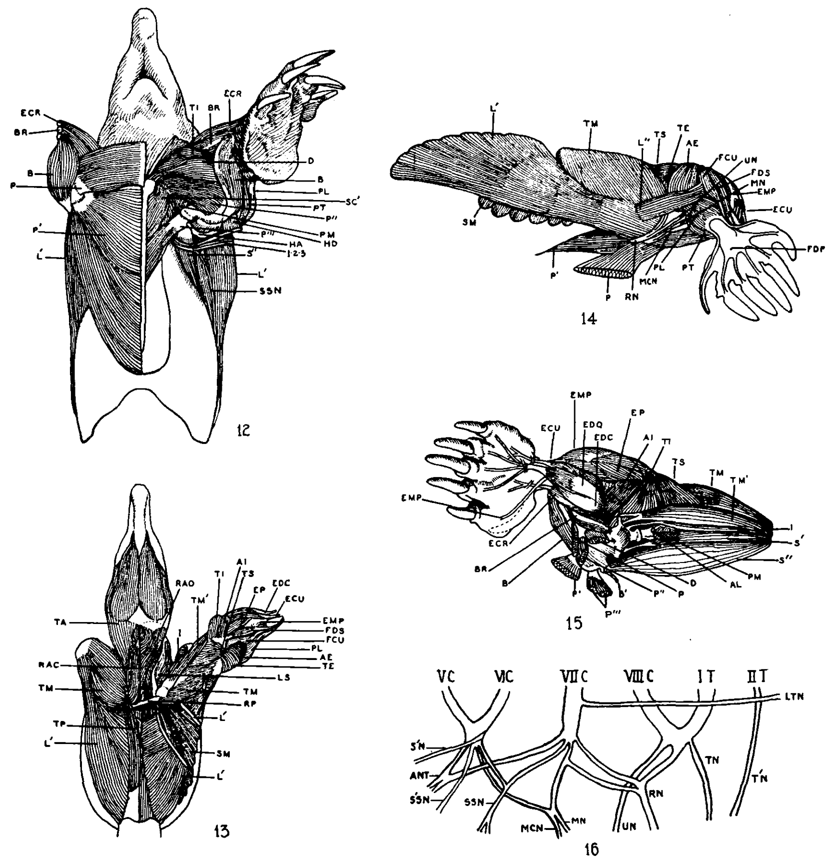

FIG. 12. Ventral aspect of muscles of forelimb of mole.
FIG. 13. Dorsal aspect of muscles of forelimb of mole.
FIG. 14. Lateral aspect of muscles of right forelimb of mole.
FIG. 15. Medial aspects of muscles of right forelimb of mole.
FIG. 16. Diagram of left brachial plexus of mole, showing the origin of only the nerves to the muscles of the forelimb.

(Interpretation of legends is given in list of abbreviations, page 41.)

element is provided, accessory ligaments are present. These extend from the margin of the sigmoid cavity of the radius to the lateral epicondyle and adjacent margin of the semilunar notch of the ulna and from the latter to the medial epicondyle. The movements which occur are limited to flexion and extension.

Although the proximal extremities of the radius and ulna articulate, forming what may be termed a superior radio-ulnar articulation, it is doubtful whether any pronation or supination occur here.

The **Wrist-joint** (fig. 3C) is also a double articulation. It consists of two facets on the distal extremity of the radius, which articulate with the navicular and lunate bones, and articular surfaces on the distal extremity of the ulna, which articulate with the triquetral and pisiform bones. According to Dobson (loc. cit., p. 164) the pisiform bone does not enter into the wrist-joint. However, in Scalops aquaticus this is a well defined articulation and the articular surfaces are of such a nature as to form somewhat of an interlocking device thus adding security to the joint, and permits only flexion and extension. It is provided with an articular capsule which is reinforced by means of short, strong ligaments.

An inferior radio-ulnar articulation does not occur, although ligaments connect the distal extremities of the radius and ulna.

In the remaining articulations of the manus flexion and extension occur freely, the digits maintaining a position of abduction, that is spread apart. Moreover, the normal position of the digits when the mole is at rest is extension rather than slight flexion as in man thus giving the manus its shovel-like appearance. The base of the falciform bone is held firmly against the lateral side of the navicular bone by means of short, strong ligaments. It is attached throughout most of its length to the side of the pollex by a fold of skin.

MUSCULATURE

The origin, insertion and nerve supply of the muscles of the forelimb were observed by means of dissection, whereas their actions were determined by applying the principles of leverage, that is, by noting their points of attachment on the articulated limb, by pulling upon the dissected muscles and observing the resulting movements. Observations were made on the movements of the living animal, although these yielded unsatisfactory results as regard primary muscle action. However, the fundamental movements of the various segments of the forelimb during the digging process were thereby ascertained. Naturally, the question arises as to the homology of these muscles with those of higher mammals. Notwithstanding the difficulties encountered due to the numerous modifications and morphological adaptations exhibited by the majority of these muscles, this was, for the most part, readily determined by employing the criteria of nerve supply and morphology, including points of attachment. However, in a few instances, notably the pectoralis minor and subclavius muscles, their homology is questionable and the writer may be in error in employing these names. As regard the subclavius Dobson observed and described it as such for the star-nosed mole, whereas he made no mention of the muscle described in this paper as the pectoralis minor but applied this name to the posterior deep portion of the pectoralis major, with which it is generally conceded to be homologous.

In addition to the proper appendicular muscles of the fore-limb there are two cutaneous muscles attached to the humerus, namely, the humero-dorsalis and humero-abdominalis. These are portions of the cutaneous maximum or panniculus carnosus which serves primarily to move the integument. However, since these two muscles are attached to the humerus (origin) and to the skin of the back and abdomen (insertion) their action may be reversible, that is they may serve to move the humerus.

The **Humero-dorsalis** (fig. 12) arises from the shaft of the humerus under cover of the biceps brachii muscle and inserts into the skin on the sides of the back. It may serve indirectly to flex the humerus, that is, draw it backward.

The **Humero-abdominalis** (fig. 12) arises from the bicipital ridge of the humerus under cover of the insertion of the posterior superficial pectoralis major and inserts into the skin on the sides of the abdomen. It may likewise serve to flex the humerus.

The **Pectoralis major** (figs. 12, 14, 15) is a large, complex muscle which extends from the ventral aspect of the thorax to the humerus. It is divisible into four parts, two of which are superficial and two deep. The anterior superficial pectoralis (pars clavicularis of man) (P) arises from the anterior end of the manubrium and from a raphè craniad to it and inserts into the pectoral ridge of the humerus. This raphè forms a common tendon of origin for both anterior superficial pectorals thus providing a continuous band stretching across between both forelimbs and serving to hold them in position. The posterior superficial pectoralis (pars sternocostalis of man) (P′) takes origin from the entire length of the sternum and is inserted into the bicipital ridge of the humerus. The anterior deep pectoralis (pars prescapularis; pectoralis parvus) (P″) arises from the anterior surface of the clavicle and inserts into the pectoral ridge of the humerus. The posterior deep pectoralis (pectoralis minor of man) (P′″) arises from the manubrium and costal cartilages and inserts into the bicipital ridge of the humerus. The action of the pectoralis major as a whole is to adduct the humerus. Its separate divisions when acting as functional units perform the following movements: the anterior superficial and deep portions pull the humerus forward while the posterior superficial and deep portions pull it backward.

The **Subclavius** muscle (fig. 12) is situated deep to the pectoralis major where it arises from the side of the manubrium and the first few costal cartilages. It passes forward to be inserted into the subclavian tubercle of the clavicle. It retracts the clavicle, that is, pulls it backward, and like its homologue (?) in man subserves the function of bracing the clavicle against the manubrium.

The **Pectoralis minor** muscle (figs. 12, 15) lies deep to the subclavius. It takes origin from the manubrium and is inserted into the posterior aspect of the lateral end of the clavicle, the acromioclavicular ligament and the acromion of the scapula. It retracts the shoulder-girdle. As mentioned previously the homology of this muscle is questionable. The writer ventures the suggestion that it may represent a muscle occasionally appearing in man and described in Quain's Anatomy

('23, p. 104) as the sterno- or chondroscapularis (subclavius posticus), which is said to arise from the manubrium and first costal cartilage and after passing behind the clavicle and normal subclavius to be inserted into the superior border of the scapula.

The **Trapezius** muscle (fig. 13) consists of two portions, anterior and posterior. The anterior trapezius (cranial part of human trapezius) arises from the occipital bone and inserts into the posterior border of the scapula. The posterior trapezius (caudal part of human trapezius) arise from the pelvic and sacral bones and inserts into the spine of the scapula. The anterior trapezius serves to pull the scapula forward and the posterior trapezius to draw it backward.

The **Rhomboideus** muscle (fig. 13) is also divisible into two portions, namely, anterior and posterior. The rhomboideus anterior is in turn divisible into cervical and occipital portions. The cervical portion (RAC) arises from the ligamentum nuchae, which is here ossified, and inserts into the posterior border of the scapula. It serves to draw the scapula forward (protract) and medial (adduct). The occipital portion lies partly under cover of the anterior trapezius. It takes origin from the occipital bone and is inserted into the ligamentum nuchae. It acts as a brace for the ligamentum nuchae thereby giving it support for the action of the cervical portion. The rhomboideus posterior arises from a common tendon, in conjunction with its fellow of the opposite side, which is attached to the last cervical and first thoracic vertebrae. Insertion is into the posterior border of the scapula and the action is to adduct the scapula. Moreover, with its fellow of the opposite side it serves as a ligamentous band which tends to hold the scapulae in close proximity. Dobson claims (loc. cit., p. 166) that the occipital portion of the rhomboideus anterior is "inserted into the postero-internal margin of the scapula," thus differing from the observations made by the writer.

The **Levator scapulae** muscle (fig. 13) is situated on the lateral aspect of the neck where it arises from the sides of the cervical vertebrae and inserts into the posterior border of the scapula. It protracts the scapula.

The **Serratus anterior** (magnus) muscle (figs. 13, 14) lies on the lateral aspect of the thorax where it arises by digitations from the first 8 or 9 ribs. It passes between the medial surface of the scapula and the ribs to be inserted into the posterior border of the scapula. Its chief action is to abduct the scapula, that is, pull it laterad.

The **Latissimus dorsi** muscle (figs. 12–14) is a large fan-shaped muscle situated on the side of the trunk. It takes origin from the spinous processes of the last few thoracic and all of the lumbar vetrebrae and from the dorsal surface of the sacrum. Its tendon fuses with that of the teres major muscle forming a common tendon which is inserted into the distal process (L3) on the posterior (medial) border of the humerus. The action of these muscles is to flex and abduct the humerus.

The **Tensor fasciae antibrachii** (epitrochlearis) (fig. 14) is a quadrilateral-shaped muscle arising from the tendon of the latissimus dorsi and inserting into the antibrachial fascia and olecranon process. It serves to extend the elbow-joint and to make the fascia tense.

The **Teres major** muscle (figs. 13–15) forms a pronounced muscular mass situated on the inferolateral aspect of the scapula. It arises from the entire length of the ventral border of the scapula and inserts along with the latissimus dorsi as mentioned above.

The **Teres minor** muscle (figs. 13, 15) is a long spindle-shaped muscle situated on the lateral aspect of the scapula. It is separated from the teres major muscle by means of the long head of the triceps brachii and its tendon passes to the lateral side of the acromion and acromioclavicular ligament. It arises from the ridge which forms the lower boundary of the infraspinous fossa of the scapula and inserts into the spinous process on the greater tuberosity of the humerus. It is a weak flexor and abductor of the humerus. According to Dobson (loc. cit., p. 168) this muscle "appears to be absent."

The **Infraspinatus** muscle (figs. 13, 15) is a small spindle-shaped muscle located deep on the teres minor with which it is blended. Its origin is from the infraspinous fossa of the scapula and its insertion is into the posterior margin of the clavicular facet of the humerus. It assists in flexing and abducting the humerus.

The **Supraspinatus** muscle (fig. 15) is a long fusiform muscle which arises, as its name implies, from the supraspinous fossa and inserts into the dorso-medial aspect of the neck of the humerus. Its tendon passes medial to the acromion and acromioclavicular ligament. The action of this muscle is similar to that of the infraspinatus.

The **Subscapularis** muscle (fig. 15) occupies the entire subscapular fossa of the scapula from which it takes origin. The insertion is into the bicipital ridge of the humerus. The angle of pull is such that it must be considered a flexor and abductor of the humerus.

The **Deltoid** (figs. 12, 15) is a thin, quadrilateral-shaped muscle lying under cover of the anterior superficial portion of the pectoralis major muscle. It lies parallel with the anterior deep portion of the pectoralis major with which it is blended. Its origin is from the anterior surface of the clavicle and its insertion is into the deltoid ridge of the humerus. It serves to extend the humerus and possibly to adduct it.

The **Triceps brachii** (figs. 12–15) forms a large muscular mass on the posterior aspect of the humerus. It consists of three heads, namely, a scapular (long) head, an external head and an internal head. The scapular head (Ts) arises from the ridge forming the lower boundary of the infraspinous fossa, where it separates the teres major and minor muscles. This point of origin differs from that in typical mammals in which it arises from the ingraglenoid tubercle along the axillary border and is explained on the basis of the shift in position of the humerus. The external (lateral) head (TE) is divisible into two parts, a superficial which arises from the spinous process on the greater tuberosity of the humerus and a deep which arises from the posterior margin of the articular (clavicular) facet on the greater tuberosity. The internal (medial) head (TI) arises from the groove on the posterior aspect of the shaft of the humerus. The tendon formed by the union of these heads is inserted into the expanded extremity of the olecranon process of the ulna. The action of this muscle as a whole is to extend the fore-arm at the elbow-joint while the scapular head may assist indirectly in flexing the humerus at the shoulder-joint.

The **Biceps brachii** (figs. 12, 15) is a thick, fusiform muscle lying on the anterior surface of the humerus. Its tendon of origin is strong, long and rounded (B′) and is attached to the infraglenoid tubercle of the scapula. This point of attachment presents a peculiar modification since in higher mammals the tendon of origin is attached to the opposite side of the glenoid fossa, that is, to the supraglenoid tubercle. Moreover, as mentioned above, the infraglenoid tubercle in higher forms marks the point of origin of the long head of the triceps. In conformity with the change of position of the humerus, that is, from the adducted position to the abducted and medially rotated one, the point of origin of this muscle as well as that of the long head of the triceps has shifted in the mole. The tendon of the biceps undergoes a rather tortuous course, passing at first ventrally to gain entrance into the closed bicipital canal of the humerus, from which it emerges to curve forward through the notch separating the ridges on the medial border of the humerus. The muscle is inserted into the roughened area (bicipital tuberosity) on the medial surface of the shaft of the radius. As in typical mammals this muscle serves primarily to flex the antibrachium at the elbow-joint. However, unlike that in most mammals, it does not supinate this region, since little or no supination occurs. Moreover, in view of the course of its tendon of origin and of its direction of pull, it may possibly adduct the brachium.

The **Brachialis** (figs. 12, 15) forms a rounded, muscular mass which occupies the fossa under the greater tuberosity and the spiral groove on the antero-lateral surface of the humerus. Its tendon of insertion is attached to the tuberosity of the ulna. It assists the biceps in flexing the antibrachium at the elbow-joint.

The **Anconeus externus** (figs. 13, 14) is a triangular-shaped muscle which arises from the spinous process on the lateral epicondyle and tendon of the teres major muscle. It inserts into the lateral surface of the olecranon process of the ulna and assists the triceps in extending the antibrachium at the elbow-joint.

The **Anconeus internus** (figs. 13, 15) is situated on the medial aspect of the humerus where it arises from the spinous process on the medial epicondyle and inserts into the expanded tip of the olecranon process. It also assists in extending the antibrachium.

The **Pronator teres** (figs. 12, 14) is situated on the volar surface of the fore-arm between the biceps and palmaris longus. It arises from the anterior aspect of the medial epicondyle of the humerus between the styloid process and the facet, and is inserted into the medial surface of the shaft of the radius. Its chief action is to assist in flexing the antibrachium. It is doubtful whether it produces any pronation of the fore-arm, since the nature of the articulation tends to limit such a movement.

The **Palmaris longus** (figs. 12–14) forms a thick muscular mass on the volar surface of the antibrachium where it lies parallel with and medial to the pronator teres. It arises from the styloid process of the medial epicondyle of the humerus. It gives off two tendons, one of which passes lateralward to be inserted into the palmar surface of the falciform bone, the other passes medialward to be inserted into the ulnar side of the distal phalanx of the fifth digit. It serves primarily to increase the width of the manus by abducting the falciform bone and the fifth digit, although it also acts to flex the manus and the antibrachium.

The **Flexor carpi ulnaris** (figs. 13, 14) lies medial to the palmaris longus on the volar surface of the antibrachium. It arises by fleshy fibers from the medial surface of the keeled olecranon process and inserts into the pisiform bone. It assists in flexing the manus at the wrist-joint.

The **Flexor digitorum sublimis** (figs. 13, 14) lies deep to but is larger than the flexor carpi ulnaris. It takes origin on the medial surface of the olecranon process and the shaft of the ulna. Its tendon passes laterally under that of the flexor carpi ulnaris to gain the palmar aspect of the manus where it intimately blends with the underlying tendon of the flexor digitorum profundus. It assists in flexing the manus and may indirectly assist the latter muscle in flexing the digits.

The **Flexor digitorum profundus** (fig. 14) presents a very interesting fossorial adaptation. It consists of two heads of origin, one of which is muscular and the other tendinous. Its muscular origin is from the anterior border of the shaft of the ulna, while its tendinous origin is from the facet on the medial epicondyle of the humerus. The tendinous portion is quite pronounced forming a wide, strong band which is joined obliquely by the muscular portion. It enters the palm of the manus by passing through the smooth groove formed by the proximal row of the carpal bones. Within the palm it divides into five tendinous slips which insert into the terminal phalanges of the digits. The action of this muscle is threefold, namely, to flex the manus and the digits, and to exert a ligamentous action on the manus and digits by checking over-extension, thus increasing the efficiency of the shovel-like action of the manus.

The **Extensor carpi radialis** (figs. 12, 15) is a small, fusiform muscle lying on the radial side of the dorsal surface of the antibrachium. It arises from the spinous process of the lateral epicondyle of the humerus and inserts into the bases of the second and third metacarpal bones. Its tendon is crossed by that of the extensor ossis metacarpi pollicis and is held down firmly as it passes over the carpus by a ligamentous band or annular ligament. It assists in extending the manus at the wrist-joint.

The **Extensor digitorum communis** (figs. 13, 15) forms a prominent muscular mass along the middle of the dorsal surface of the antibrachium. It arises from the spinous process of the lateral epicondyle of the humerus. It breaks up into tendons which, after passing through an annular ligament, insert into the terminal phalanges of the lateral four digits. It extends the manus and digits.

The **Extensor (minimi) digiti quinti proprius** (fig. 15) is a small fusiform muscle lying on the ulnar side of the extensor digitorum communis with which it is intimately fused. It arises from the spinous process of the lateral epicondyle of the humerus and inserts by means of a slender tendon into the terminal phalanx of the fifth digit. It serves to extend the fifth digit and assists in extending the manus.

The **Extensor carpi ulnaris** (figs. 13–15) is a fusiform-shaped muscle lying on the ulnar side of the extensor digiti quinti. It arises by two heads, one from the lateral epicondyle of the humerus and one from the expanded tip of the olecranon process. Its tendon of insertion is attached to the distal extremity of the ulna, from which it passes forward and divides into two tendons which are attached to the bases of the fourth and fifth metacarpals. It assists in extending the manus at the wrist-joint.

The **Extensor pollicis et indicis** (figs. 13, 15) is a triangular-shaped muscle situated on the ulnar side of the extensor carpi ulnaris where it arises from the tip of the olecranon process. Its small, thin tendon passes obliquely under that of the extensor digitorum communis through the annular ligament to the dorsal surface of the hand where it divides into two tendons which insert into the terminal phalanges of the pollex and index finger, respectively. It serves, as its name implies, to extend the pollex and index finger (2nd. digit) and also indirectly the manus.

The **Extensor ossis metacarpi pollicis** (extensor pollicis brevis) (figs. 13–15) lies deep to the extensor pollicis et indicis on the ulnar side of the dorsal surface of the antibrachium. It arises by two heads, one from the lateral surface of the keeled olecranon process and shaft of the ulna, the other from the lateral surface of the radius. Its tendon passes obliquely laterad through a groove on the shaft of the radius under cover of the tendons of the extensor digitorum communis, thence it passes over the tendon of the extensor carpi radialis to the radial side of the base of the first metacarpal. It extends the manus at the wrist-joint.

No intrinsic muscles were discernible in the manus.

Nerve Supply—The muscles of the forelimb are innervated for the most part by nerves which branch from the brachial plexus, a diagram of which is shown in figure 16. The pectoralis major and minor muscles are supplied by the anterior thoracic nerves, which arise from the 5th, 6th and 7th cervical nerves and pass ventrally to enter the muscles. The humero-dorsalis and humero-abdominalis muscles are supplied by branches from the 1st and 2nd thoracic nerves which pass laterad and form a plexus on the deep surface of the muscles. The nerve which supplies the subclavius muscle arises from the 5th and 6th cervical nerves. It passes directly craniad along the supero-lateral surface of the manubrium to the posterior surface of the clavicle where it terminates in the muscle.

The levator scapulae and rhomboideus muscles receive their nerve supply from branches of the cervical plexus. These branches ascend along the cranial border of the levator scapulae, giving off twigs in their ascent, to terminate in the rhomboideus muscles. The levator scapulae is, in addition, supplied by a branch from the long (posterior) thoracic nerve, which arises from the 7th cervical nerve. It passes caudad on the surface of the seratus anterior muscle which it also supplies. The trapezius is likewise innervated by some twigs from the cervical plexus and by the spinal accessory nerve. The latter nerve courses along the lateral margin of the trapezius anterior muscle, giving off twigs, and terminating in the trapezius posterior.

The supraspinatus, infraspinatus, teres minor and deltoid muscles are supplied by a nerve which arises from the 5th and 6th cervical nerves. This nerve probably represents the combined suprascapular and axillary nerves common to mammals. It extends laterad from its point of origin and enters the supraspinatus muscle where it gives off branches to the other muscles.

The subscapularis, latissimus dorsi and teres major muscles are supplied by the subscapular nerves (fig. 12) which arise from the 5th, 6th and 7th cervical nerves.

The biceps brachi and brachialis muscles receive their supply through the musculocutaneous nerve which takes origin from the 5th, 6th and 7th cervical nerves. This nerve is the most anterior of the four nerves (fig. 14) which curve round the lateral aspect of the axilla.

The tensor fasciae antibrachii, anconeus internus and externus, triceps brachii and the extensor muscles of the antibrachium are supplied by the radial nerve which arises from the 7th and 8th cervical and 1st thoracic nerves. It curves round the lateral boundary of the axilla where it is the most posteriorly situated of the four nerves observed at this point (fig. 14). It enters the brachium just posterior to the anconeus externus and after giving off branches to the extensor group of muscles of the brachium enters the antibrachium by curving round the spinous process of the lateral epicondyle.

The flexor group of muscles of the antibrachium are supplied by the median and ulnar nerves. The median nerve arises from the 5th, 6th and 7th cervical nerves, passes laterad just posterior to the musculocutaneous nerve (fig. 14), passes into the brachium deep to the anconeus externus and enters the antibrachium through the supracondylar foramen. It supplies all the volar antibrachial muscles with the exception of the flexor carpi ulnaris. The ulnar nerve arises from the 8th cervical and 1st thoracic nerves, runs parallel with and between the median nerve anteriorly and the radial nerve posteriorly (fig. 14) and enters the antibrachium, by curving round the spinous process of the medial epicondyle, where it supplies the flexor carpi ulnaris and sends some twigs into the flexor digitorum profundus.

DISCUSSION AND SUMMARY

The most striking morphological adaptations exhibited by the bones of the forelimb of the mole may be summarized as follows: the cuboidal form of the clavicle and its articulation with the humerus rather than with the scapula; the elongation of the scapula; the broadening of the humerus, the pronounced development of its processes for muscular attachments, the closure of its intertubercular groove, the presence of a clavicular facet and the shift in position of the head to its dorsal surface; the presence of a sigmoid articular surface on the proximal end of the radius; the elongation and expansion of the olecranon process, the deep semilunar notch and carpel articulation of the ulna; the increased relative width of the bones of the manus; the presence of an accessory falciform bone and the development of strong, nail-like claws.

As regard the position of the bones in the articulated forelimb the most salient features are as follows: the craniad shift in position of the shoulder-girdle due to the elongation of the manubrium; the rotation of the scapula resulting in its original dorsal border facing caudad and its glenoid cavity directed craniad; the abduction of the humerus to a ninety-degree angle accompanied by extreme medial rotation resulting in its original lateral border facing craniad and its distal end projecting antero-laterad; the lack of a distal radio-ulnar articulation; the uncrossed position of the radius and ulna with the radius situated antero-mediad and the ulna postero-laterad so that their original volar surfaces face postero-mediad and the palm of the manus postero-laterad, with the pollex directed caudad and the fifth digit craniad.

The chief fossorial adaptations manifested by the muscles of the forelimb of the mole are such features as the following: the great development of certain muscles, as for example the teres major, latissimus dorsi, pectoralis major and palmaris longus, which serve to put the limb in its peculiar position as well as into action; the absence of certain muscles normally present in the mammalian forelimb, as for example, the mastoideohumeralis (brachiocephalicus), scapulohumeralis posticus (capsularis), coracobrachialis, brachioradialis, supinator, pronator quadratus, abductor pollicis longus, flexor carpi radialis and the intrinsic muscles of the manus; the acquisition of new points of origin of the biceps brachii and the long head of the triceps brachii and the change in action of certain muscles, as for example, the occipital portion of the rhomboideus anterior, the teres major and deltoid due to alteration of position of the forelimb.

It is evident that the normal position of the brachium of the mole, that is abduction accompanied by extreme medial rotation, is maintained by active muscular contraction. The muscles acting on the humerus to produce abduction and medial rotation are the latissimus dorsi, teres major and minor, infraspinatus, supraspinatus and subscapularis, assisted by the pectoralis major in rotation.

During the excavation of the underground tunnels the forelimb of the mole alternately swings backward and forward with great strength and rapidity, much in the same fashion as the swimming movements of man. The backward movement is, of course, the more powerful since it supplies the impetus resulting in pushing the earth aside, whereas, the forward swing serves to place the limb in a favorable position for the backward thrust. During the forward swing the brachium, antibrachium, manus and digits are extended and in the backward thrust these parts are powerfully flexed. Concurrent with these fundamental movements of the free forelimb are complimentary movements of the shoulder-girdle, that is forward (protraction) and backward (retraction), thus serving to impart added impetus to the movements of the free limb and to maintain the articular surfaces of the shoulder-joint in apposition.

The muscles acting on the various parts of the forelimb in the production of these movements are summarized as follows: extension (swinging forward) of the brachium at the shoulder-joint is produced by the anterior (superficial and deep) portion of the pectoralis major and the deltoid; flexion (swinging backward) of the brachium by the latissimus dorsi, infraspinatus, supraspinatus, teres major and minor, subscapularis, long head of the triceps brachii and the posterior (superficial and deep) portion of the pectoralis major; flexion of the antibrachium at the elbow-joint by the biceps brachii, brachialis and the volar antibrachial muscles, which arise from the medial (internal) epicondyle of the humerus (namely, pronator teres and palmaris longus); extension of the antibrachium by the triceps brachii, anconeus externus and internus and the dorsal antibrachial muscles, which arise from the lateral epicondyle of the humerus (namely, extensor carpi radialis, extensor digitorum communis, extensor digiti quinti, and in part the extensor carpi ulnaris); flexion of the manus by the volar antibrachial muscles (palmaris longus, flexor carpi ulnaris, and flexor digitorum sublimis and profundus); extension of the manus by the dorsal antibrachial muscles (extensor carpi radialis and ulnaris, extensor digitorum communis, extensor digiti quinti, extensor pollicis et indicis and the extensor ossis metacarpi pollicis); while flexion and extension of the digits are produced by the flexor and extensor digitorum muscles, respectively.

Protraction of the shoulder-girdle is brought about by the action of the trapezius and rhomboideus anterior and levator scapulae while retraction is produced by the subclavius, pectoralis minor, trapezius posterior, possibly the serratus anterior and indirectly the latissimus dorsi and posterior portion of the pectoralis major.

The nerves which supply the muscles of the forelimb exhibit no striking peculiarities other than the course which the musculocutaneous, median, ulnar and radial nerves take, namely, round the postero-lateral boundary of the axilla rather than the antero-medial as in typical mammals. The peculiar course of these nerves is indubitably due to the pronounced medial rotation of the brachium.

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ABBREVIATIONS

A—acromion
AB—ventral (axillary) border of scapula
AE—anconeus externus
AI—anconeus internus
AL—acromioclavicular ligament
ATN—anterior thoracic nerves
B—biceps brachii
B′—tendon of biceps
BR—brachialis
C—coracoid
C′—carpus
C″—capitulum
CA—capitate
CE—centrale
CF—clavicular facet
CF′—navicular facet
CP—coronoid process
D—deltoid
DB—dorsal (posterior) border
DT—deltoid tuberosity
ECR—extensor carpi radialis
ECU—extensor carpi ulnaris
EDC—extensor digitorum communis
EDQ—extensor digiti quinti proprius
EJ—elbow-joint
EMP—extensor ossis metacarpi pollicis
EP—extensor pollicis et indicis
F—foramen
F′—facet
F″—fossa
FA—falciform bone
FCU—flexor carpi ulnaris
FDP—flexor digitorum profundus
FDS—flexor digitorum sublimis
G—groove
GF—glenoid fossa
GM—greater multangular
GT—greater tuberosity
H—humurus
H^1—hook-like process
H^2—hamate
HA—humeroabdominalis
HD—humerodorsalis
HF—humeral facet
I—infraspinatus
IF—infraspinous fossa
IG—intertubercular groove (canal)
IT—infraglenoid tubercle
L—lunate
L′—latissimus dorsi
L″—tensor fasciae antibrachii
L_1—medial lamina on lesser tuberosity
L_2—lateral lamina (bicipital ridge)
L_3—point of insertion of latissimus dorsi and teres major
LE—Lateral epicondyle
LF—lunate facet
LM—lesser multangular
LS—levator scapulae
LTN—long thoracic nerve
M_{1-2}—metacarpal bones
MCN—musculocutaneous nerve
MN—median nerve
N—navicular
N_{1-2}—notch
NF—navicular facet
NS—median, ulnar and radial nerves
OF—olecranon fossa
OP—olecranon process
P—anterior superficial pectoralis
P′—posterior superficial pectoralis
P″—anterior deep pectoralis
P‴—posterior deep pectoralis
Pb—pisiform
P_{1-3}—phalanges
PL—palmaris longus
PM—pectoralis minor
PR—pectoralis ridge
PT—pronator teres
R—radius
RAC—rhomboideus anterior (cervical portion)
RAO—rhomboideus posterior (occipital portion)
RF—Radial fossa
RF′—radial facet
RN—radial nerve
RP—rhomboideus posterior
S—scapula
S′—supraspinatus
S″—subscapularis
SC—sigmoid cavity
SC′—subclavius
SF—sternal facet
SF′—supracondylar foramen
SF_1—supraspinous fossa
SF_2—subscapular fossa
SJ—shoulder-joint
SM—serratus magnus (anterior)
SN—semilunar notch
S^1N—nerve to subclavius muscle
SP—spine
SS—suprascapula
SSN—suprascapular nerve
S′SN—subscapular nerve
ST—sternum
ST′—subclavian tubercle
T—tuberosity
TA—trapezius anterior
TE—external head of triceps brachii
TI—internal head of triceps brachii
TM—teres major
TM′—teres minor
TN-T′N—nerves to humerodorsalis and humeroabdominalis
TP—trapezius posterior
TR—triquetral
TRO—trochlea
TS—long (scapular) head of triceps brachii
U—ulna
UF—ulnar facet
UN—ulnar nerve